SIZE-BASED TRENDS AND MANAGEMENT IMPLICATIONS OF MICROHABITAT UTILIZATION BY BROWN TREESNAKES, WITH AN EMPHASIS ON JUVENILE SNAKES

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Abstract: The brown treesnake (*Boiga irregularis*, or BTS), a costly invasive species, has been the subject of intensive research on Guam over the past two decades. The behavior and habitat use of hatchling and juvenile snakes, however, remain largely unknown. We used a long-term dataset of BTS captures (N = 2,415) and a dataset resulting from intensive sampling within and immediately around a 5-ha fenced population (N = 2,541) to examine habitat use of BTS. Small snakes were almost exclusively arboreal and that they appeared to prefer tangantangan (*Leucaena leucocephala*) habitats. In contrast, large snakes used arboreal and terrestrial habitats in roughly equal proportion, and were less frequently found in tangantangan. Among snakes found in trees, there were no clear size-based preferences for certain heights above ground, nor for size-based choice of perch diameters. We discuss these results as they relate to management and interdiction implications for brown treesnakes on Guam and in potential incipient populations on other islands.

Key Words: *Boiga irregularis*, brown treesnake, Guam, habitat use, invasive species, interdiction, Saipan, visual searching.

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INTRODUCTION

Among invasive species worldwide, the brown treesnake (*Boiga irregularis*, or BTS) is routinely upheld as an archetypical invasive species, largely due to its decimation of the forest avifauna of Guam after its accidental introduction to the island in the 1940s (Savidge 1987, Rodda et al. 1999b). The history of this introduction and its environmental and economic effects has recently been subject to an updated review by Rodda and Savidge (2007). Despite the wide acceptance of the BTS as an exemplar of the ecological havoc that can be wreaked by a vertebrate invader, there are still many aspects of this species' biology that are poorly understood.

Among the poorly known aspects of BTS biology is the habitat use and behavior of hatchling and juvenile snakes. On Guam, BTS hatch at about 375 mm snout-vent length (SVL), and are mature at 950-1050 mm SVL (Savidge et al. 2007). While the advent of miniature radiotransmitters has revolutionized the study of secretive, cryptic snakes by allowing multiple re-locations of the same individual over time (Shine and Bonnet 2000), juvenile BTS are too small (about 4-8 g at hatching) to allow surgical implantation of transmitters with sufficient battery life for assessment of habitat use. Furthermore, until recently there was no proven means of reliably locating small BTS in complex forested environments on Guam. Traps baited with live mice (*Mus musculus*) are the primary control tool currently in use on Guam (Rodda et al 1999a, Vice et al. 2005). However, these traps are largely ineffective for snakes <850 mm SVL (Rodda et al. 2007), and thus only capture a segment of the population. In contrast, recent research indicated that visual searching by trained personnel is effective for detecting snakes across the range of BTS body sizes on Guam, including hatchlings and juveniles (Rodda et al. 2007).

Subjective impressions of various observers on Guam over the years suggest that small snakes tend towards being arboreal, while the largest snakes were more prevalent on the ground. Similarly, small snakes are often inclined to be more common in stands of introduced tangantangan (*Leucaena leucocephala*). However, these anecdotal observations have been offered by many different individuals of variable searching ability, and observations are additionally subject to variation in habitat types, temporal changes in prey availability and snake behavior, and other contributors to variability in snake detectability. In the face of these potential biases, it is difficult to quantify differential behavior and habitat use between small (<850 mm SVL, roughly the size at which ~50% of snakes become trappable; Rodda et al. 2007) and large (≥850 mm SVL) snakes. One possible solution is to examine data from observations of BTS over many years, allowing for a large sample size and thus more rigorous analyses. However, historical datasets may be subject to the same types of observer, habitat, and temporal bias as are the anecdotal impressions mentioned above, rendering their utility somewhat doubtful.

We analyzed data from both island-wide historical and intensive site-specific visual surveys for BTS. Our goals were to: (1) assess the concordance between these types of datasets to determine whether reliable conclusions can be made from potentially biased historical data, (2) analyze habitat use of small versus large snakes, and (3) discuss management implications of these results.

METHODS

We used two large datasets of BTS observations on Guam. We did not use any data resulting from trap captures of BTS, as these captures indicate height at which a trap was set and other trap placement characters, rather than independent instances of habitat choice by BTS. The first dataset was a historical (1988-2003) dataset of captures and observations resulting from visual surveys on Guam (hereafter referred to as the HIST dataset). This dataset comprised 2,415 visual observations of BTS detected island-wide, including targeted searches in numerous habitat types as well as incidental observations while conducting other fieldwork (black bars in Figure 1). Of these observations, 2,110 records included body size (total length) of the snake, 2,336 records included vertical height of the snake when first observed, 1,270 records included perch diameter (diameter of the perch upon which the snake was found, for arboreal individuals only), and 2,381

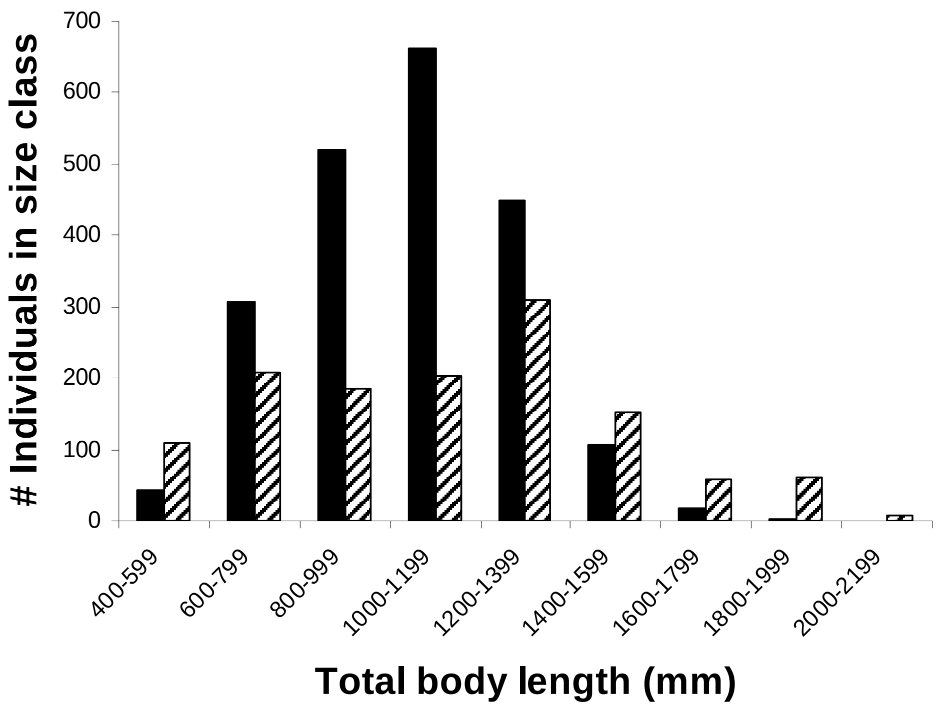


Figure 1. Sample sizes of BTS captures in the datasets used in analyses. Black bars indicate data from the HIST dataset, while hatched bars indicate data from the NWFN dataset.

records included the substrate on which the snake was first observed, including identification of the species of tree used by arboreal snakes. Body sizes were measured in the case of snakes that were captured, or estimated to the nearest 100 mm by experienced BTS biologists for snakes that could not be captured.

The second dataset was from intensive sampling from 2004-2007 in and immediately around a geographically closed population at Northwest Field North, on Andersen Air Force Base (Rodda et al. 2007). Briefly, the closed population is a 5-ha fenced plot that is impermeable to BTS immigration or emigration. This dataset included 2,541 observations of 328 individuals (hereafter referred to as the NWFN dataset; hatched bars in Figure 1). For the purposes of these analyses, we considered each capture of an individual to be an independent observation of habitat use, and thus we included multiple observations of individuals. Of these observations, 1,294 records included body size of the snake, 1,909 records included vertical height of the snake when first observed, 1,602 records included perch diameter (for arboreal individuals only), and 1,897 records included the type of perch, including identification of the species of tree used by arboreal snakes.

Means are reported ± one standard deviation. Data were $\log_{10}$-transformed when necessary to meet assumptions of normality in linear analyses. We used linear regression to analyze the amount of variation in perch diameter and vertical heights used by snakes as a function of snake body size.

RESULTS

Mean total body length of BTS in the HIST dataset was 997 ± 238 mm and ranged from 400 to 1,900 mm. Over 90% of small snakes were found in trees (black bars in Figure 2), while mean length of BTS found on the ground was 1,181 ± 179 mm total length, which is ~18% larger than the overall average. Conversely, the proportion of individuals in tangantangan decreased with increasing body length (black bars in Figure 3); mean total length of BTS found in tangantangan was 900 ± 214 mm, which is ~10% smaller than the overall average. Whilst use of terrestrial habitats was dominated by large snakes and use of tangantangan by small snakes, medium-sized snakes were somewhat more likely to be found on fences (Figure 4); mean body length of snakes on fences was 1,005 ± 211 mm. Among snakes in vegetation, mean perch diameter was 18.2 ± 30.2 mm and ranged from 1 to 950 mm.

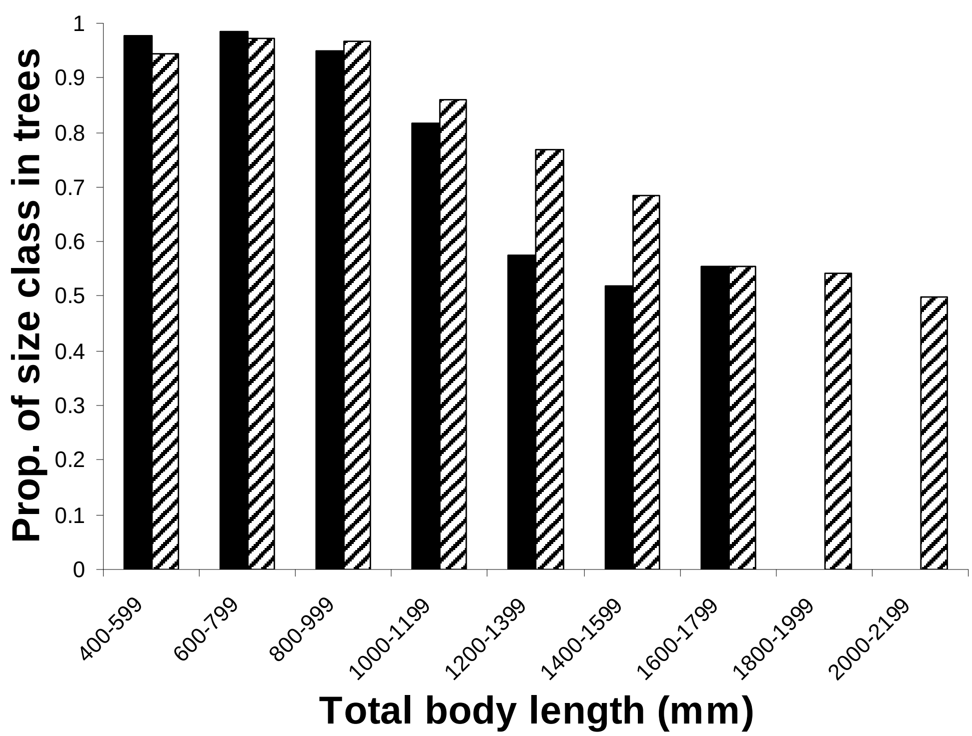


Figure 2. The proportion of BTS of various size classes that were encountered in trees during visual surveys on Guam. Black bars indicate data from the HIST dataset, while hatched bars indicate data from the NWFN dataset.

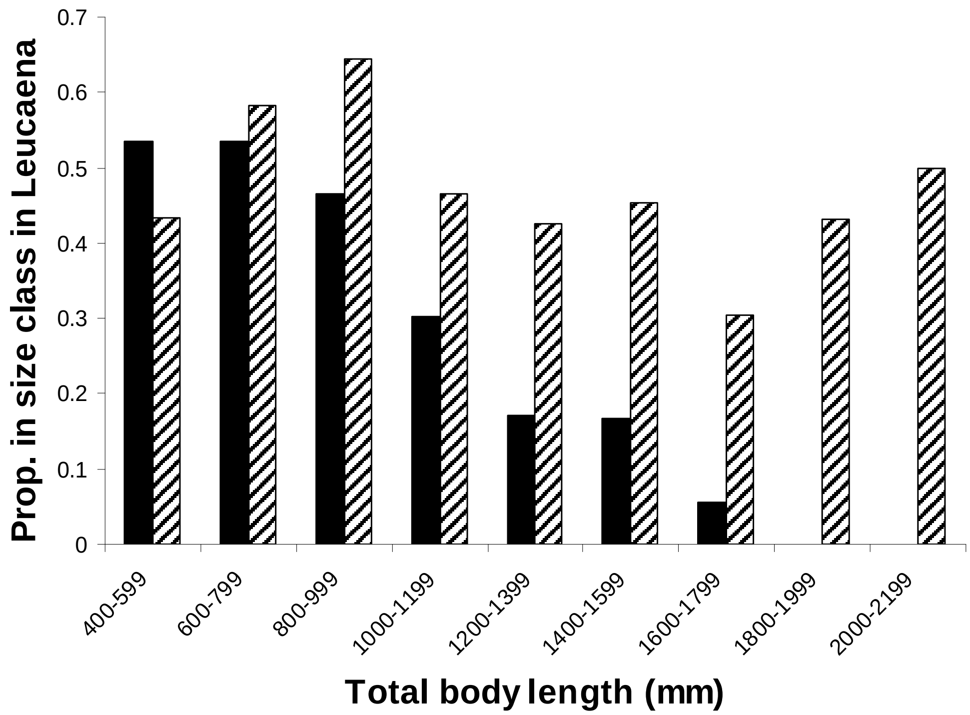


Figure 3. The proportion of BTS of various size classes that were encountered in tangantangan during visual surveys on Guam. Black bars indicate data from the HIST dataset, while hatched bars indicate data from the NWFN dataset.

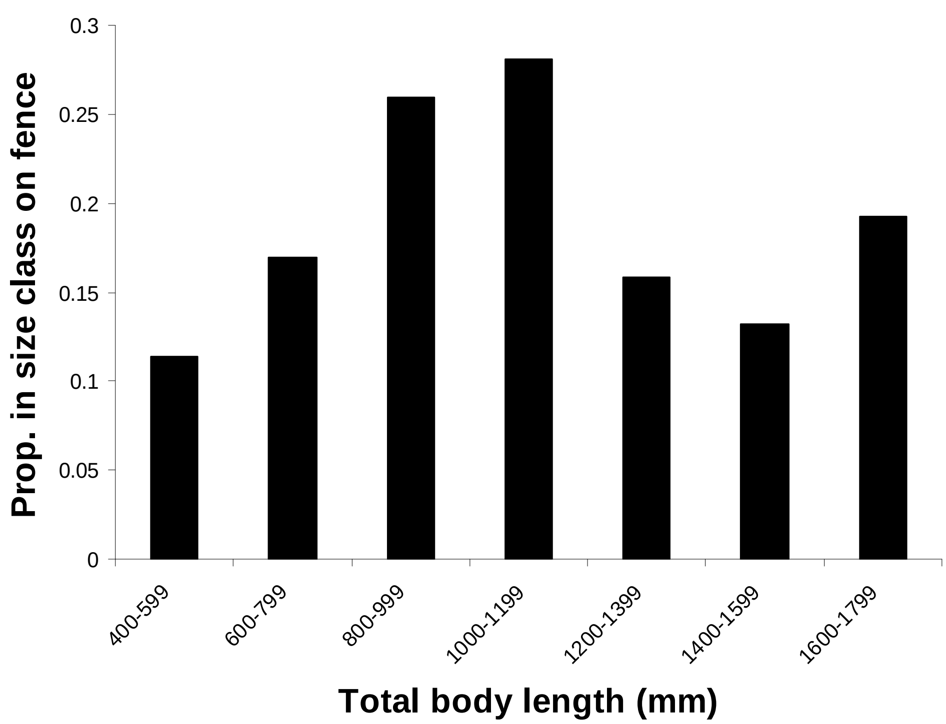


Figure 4. The proportion of BTS of various size classes that were encountered on fences during visual surveys on Guam. All data are from the HIST dataset.

Body length was a poor predictor of perch diameter, with variation in body size explaining <1% of variation in perch diameter (perch diameter $\log_{10}$-transformed, $F = 6.73$, $p = 0.01$, $r^2 = 0.0062$; solid diamonds in Figure 5). Among snakes in trees (i.e., those that were not on the ground and not on fences), total body length was also unrelated to vertical height of snakes when first observed (vertical height $\log_{10}$-transformed, $F = 3.04$, $p = 0.081$, $r^2 = 0.0027$; solid diamonds in Figure 6.)

Mean total body length of BTS in the NWFN dataset was 1,117 ± 373 mm and ranged from 405 to 2,240 mm; this dataset included 67 captures of BTS that were longer than the longest snake in the HIST dataset. As with the HIST dataset, >90% of small snakes were found in trees (hatched bars in Figure 2), and the mean length of BTS found on the ground was 1,399 ± 337, or ~24% larger than the overall average. Mean length of BTS in tangantangan was 1,069 ± 365 mm total length, ~4% smaller than the overall average (hatched bars in Figure 3); the tendency for decreased use of tangantangan use by large snakes was not as strong as for the HIST dataset. Because the NWFN dataset was largely from forested habitats with a boundary barrier that repelled climbing attempts by snakes, there were few observations of snakes on fences and thus no basis for comparison with HIST. Mean perch diameter of snakes in vegetation was 15.1 ± 26.4 mm and ranged from 1 to 500 mm. Similar to the results for the HIST dataset, total body length was related to perch diameter but explained <6% of variation in perch diameter (perch diameter $\log_{10}$-transformed, $F = 62.63$, $p < 0.0001$, $r^2 = 0.057$; hollow circles in Figure 5). Total body length was once again unrelated to vertical height of snakes when first observed in trees (vertical height $\log_{10}$- transformed, $F = 0.799$, $p = 0.371$, $r^2 = 0.0008$; hollow circles in Figure 6).

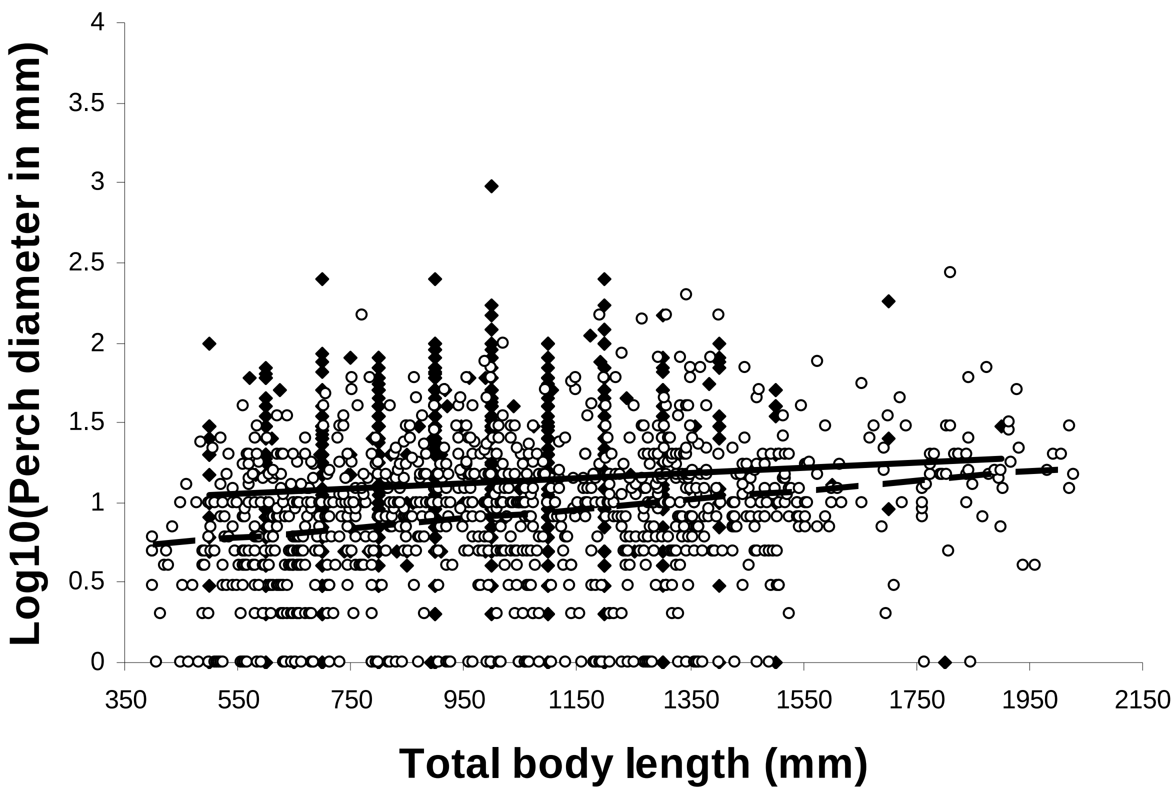


Figure 5. Perch diameter ($\log_{10}$-transformed) of BTS on Guam when first observed as a function of their total body length, with lines of best fit. Solid diamonds and solid line indicate data from the HIST dataset ($r^2 = 0.006$), hollow circles and dashed line indicate data from the NWFN dataset ($r^2 = 0.057$).

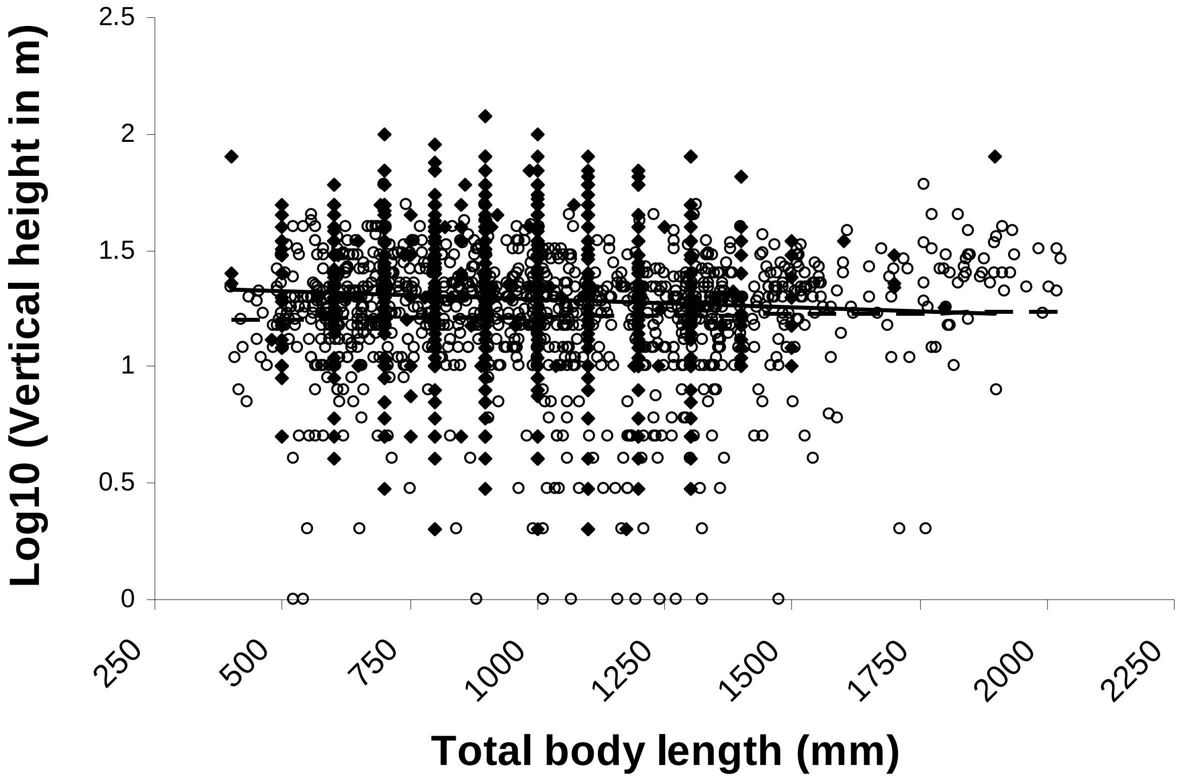


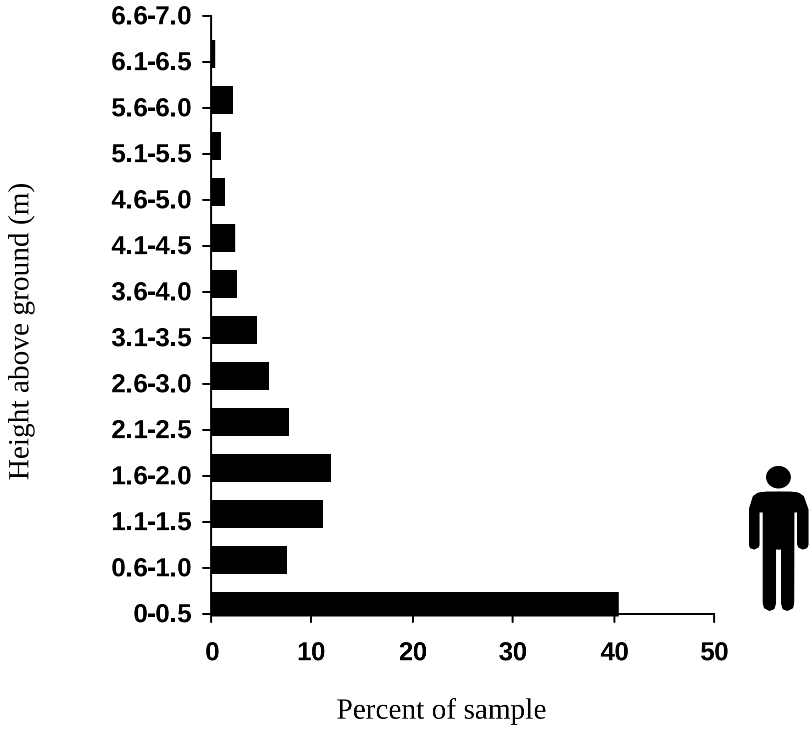
Figure 6. Vertical height ($\log_{10}$-transformed) of BTS on Guam when first observed as a function of their total body length, with lines of best fit. Solid diamonds and solid line indicate data from the HIST dataset ($r^2 = 0.003$), hollow circles and dashed line indicate data from the NWFN dataset ($r^2 = 0.001$).

DISCUSSION

Research on cryptic, nocturnal species such as BTS is often complicated by observer bias and poorly quantified detectability of different ages, sexes, or stages of the target organism. This is certainly true for BTS, as there is a great deal of inter-observer variability in the ability to find snakes via visual searches (Rodda and Fritts 1992) and rates of visual sightings are often only weakly correlated with abundance as determined by analysis of mark-recapture data (Rodda et al. 2005). However, we feel that many of the conclusions discussed below are robust to such sampling problems. For example, recent data suggest that nocturnal visual surveys are effective in detecting BTS of all body size classes (Rodda et al. 2007), such that our use of proportions, rather than absolute counts, of snakes of different sizes in different habitats is a conservative approach. Human observers may have a bias towards detecting snakes at eye level, as snakes from 1.5-2.25 m above ground are more likely to be observed during visual searches; this could potentially bias observations of vertical habitat use. We note that the overall distribution of perch heights used by snakes in the HIST dataset was qualitatively similar to the distribution of heights observed in free-ranging snakes by Clark (1998, Figure 7). In the latter study, Clark (1998) attached thread bobbins to free-ranging BTS on Guam upon capture and then immediately released them to their original position. The trailing threads were followed the day after release and heights of the thread were measured at one meter intervals. The fact that our datasets include large sample sizes of all body size classes at various heights suggests that our use of proportional abundances was unlikely to have been biased by lack of observations for some size classes.

Having assessed the potential pitfalls of analyses based on visual observations, what can we conclude about behavior and habitat use of small

Visual Search (Guam wide)



Trailing device (Orote only)

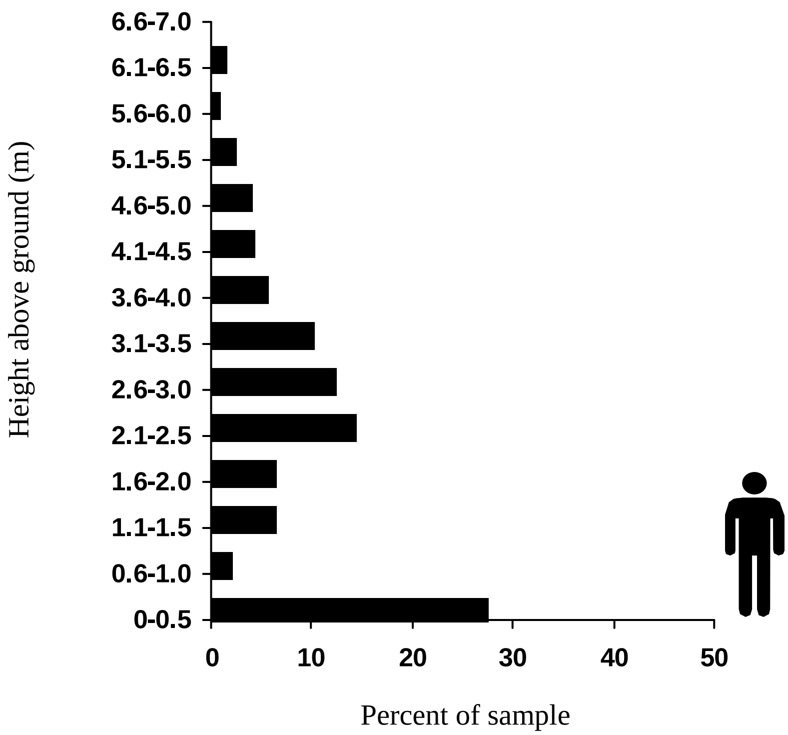


Figure 7. Comparison of observed heights of BTS when first observed in various habitats on Guam (Visual Search, from HIST dataset, on left) with vertical heights used by BTS that were released after being fitted with a thread-trailing device on Orote Peninsula, Guam (Trailing Device, on right, data courtesy C.S. Clark). Human figure added for scale.

BTS on Guam? The most striking trend was the difference between small and large snakes in their tendency to use arboreal habitats. Small snakes were overwhelmingly found in trees, while large snakes used trees and ground habitats in roughly equal proportions. Such results were highly concordant among the two datasets; snakes less than about one meter in length were almost always found in trees, but this proportion dropped to about 80% when snakes exceeded this size threshold, and decreased to roughly 50% at the largest size classes. More frequent use of terrestrial habitats by large snakes may be a foraging tactic that allows large snakes to more frequently encounter non-native small mammals (*Rattus*, *Mus*, and *Suncus*), or may represent movement for other reasons, e.g., mate-searching behavior.

Although the data indicated a difference between small and large snakes in their use of arboreal habitats, the vertical heights used by snakes were not related to snake body length. Instead, BTS appeared to use all available vegetative heights regardless of the length of the snake. Similarly, there was no clear pattern of perch diameter used by BTS as a function of body length. Small and large snakes were equally able to use perches of varying diameters, rather than being forced to use larger-diameter perches as body size increases. Brown treesnakes are extremely gracile (Rodda et al. 1999b), and even large snakes can use small-diameter perches by distributing their weight across several such perches.

Although Clark (1998) found a slight trend towards arboreal BTS using heights between 2 and 3.5 m, this may have been due to constraints on the available vegetative heights in forests on Guam, which is frequently battered by typhoons. The vertical microhabitats used by BTS from NWFN reflected the heights available to snakes; forests in the closed population were composed of young, early-successional trees that infrequently exceeded four meters in height during the sampling periods in the NWFN dataset, and this limitation was manifest in the fairly smooth upper limit to vertical heights of snakes in this dataset as compared to that observed in the HIST dataset from various forest types.

Taken together, these observations about arboreal habitat use by BTS have important management implications. Current trapping efforts typically include traps placed 1-2 m above ground level (Rodda et al. 1999a), facilitating trap-checking by humans. The apparent lack of a tendency for small BTS to prefer perches high in trees means that attempts to target such small snakes for control purposes need not include placing traps or bait stations high in trees, but that the standard operational trap heights should suffice. Logistical and safety issues associated with placing control devices high in trees might thus be avoidable for management purposes. However, we stress that this conclusion depends on the assumption that there is no inter-individual heterogeneity in the tendency to use certain perch heights. If, for example, some individuals consistently select high perches, then these individuals may avoid capture by traps placed at standard heights. Further research is required to address this question.

The HIST dataset indicates that tangantangan appeared to harbor high numbers of juvenile snakes. Detectability of BTS may be higher in tangantangan than in broad-leafed trees, as tangantangan leaflets fold up at night and observers can thus see deeper into the tree's canopy. However, observations of a high proportion of small snakes in this habitat did not appear to be an artifact of differential detectability across size classes, since medium- to large-sized snakes should have been even more visible in tangantangan. Instead, small snakes were likely keying in on the high prey densities in this habitat type. For example, Rodda et al. (2005) found that mourning geckos (*Lepidodactylus lugubris*) were present in densities >4,400/ha in some habitats on Guam, and that the density of this species can be even higher in tangantangan forests (Rodda unpublished data). These geckos are an appropriately-sized meal for juvenile BTS.

While the NWFN dataset suggested that small snakes are slightly more likely to use tangantangan than were large snakes, larger snakes also used this habitat to a greater extent than was observed in the HIST dataset. However, this was probably an artifact of the habitat available to snakes in the closed population. This area started as a scrubby plant community primarily composed of low (<1.5 m) vegetation. Erection of the snake barrier also excluded feral pigs (*Sus scrofa*) and deer (*Cervus mariannus*), allowing the vegetation inside to flourish. Tangantangan now comprises a large proportion of the forest inside the closed population. Use of this tree species by larger snakes was likely a function of its overwhelming prevalence, such that arboreal movements by large snakes were largely limited to tangantangan because there were few other choices. Habitat use by BTS in the closed population might be considered a poor example of habitat choice, since snakes were confined to a 5-ha area with limited habitat diversity. For example, Santana-Bendix et al. (1994) used radiotelemetry to determine the activity ranges of free-ranging adult BTS on Guam, and found that mean net distance moved per night was 54.7 m. If adults in the closed population were moving at even a fraction of this nightly rate, then they may frequently have "bounced" off the barrier and back into tangantangan forests where they may be detected at a higher frequency than they would be in more heterogeneous forests outside the closed population barrier.

Differential use of tangantangan by BTS of various size classes offers insights for interdiction on Guam. Habitats composed of virtually monotypic tangantangan forest are common in disturbed areas on Guam, including many forests surrounding ports of exit. These forests may harbor high densities of juvenile snakes, which are more likely to bypass traps placed on fencelines or only forest perimeters for interdiction purposes, however, see Vice and Vice (2004). Low capture rates of snakes in these traps may not necessarily reflect low BTS densities in these areas, as traps generally fail to capture small snakes (Rodda et al. 2007). While visual searches of fencelines would seem a partial solution to the size bias of traps, this is contra-indicated by the very low capture rates of small snakes on fences. Some relief from this dilemma may be afforded by the apparent avoidance of terrestrial habitats by small snakes – maintenance of a buffer of cleared ground on each side of a fenceline will likely reduce the odds of small snakes moving from forests into cargo areas and flightlines.

Heavy use of tangantangan by small, but not large, BTS in natural habitats may offer insights for detection of incipient BTS populations on islands other than Guam, especially in the Northern Mariana Islands where tangantangan is abundant. Consider a situation where a large snake is reported by an observer on Saipan, resulting in a search deployment by local agency personnel or the USGS Rapid Response Team (Stanford and Rodda 2007). If the goal is to find such a large snake by implementing the results discussed above, then searchers should remember to spend roughly equal amounts of time searching arboreal and terrestrial habitats. However, it is important to remember that the purpose of a Rapid Response deployment is not expressly to find the individual snake reported by an observer (Stanford and Rodda 2007). Deployments (and intensive search efforts by local cooperating agencies) instead function to detect and delineate incipient populations of BTS. Incipient populations are those in which reproduction has started to occur. Because gravid BTS are rarely found and eggs are extremely difficult to find (Savidge et al. 2007), evidence of reproduction is best discovered by finding hatchling and juvenile snakes. These small individuals use tangantangan extensively and can be easily detected in tangantangan at night. Assuming that BTS habitat use in an incipient population is similar to that on Guam, incipient populations could perhaps be more easily identified by concentrating search efforts near the original snake sighting, but in tangantangan habitats.

The scarcity of very small snakes in fenceline captures, as revealed by the HIST dataset, indicates that while small snakes are typically found in arboreal habitats, not all vertical substrates are equal. This result seems puzzling, as nocturnal spotlighting of chain-link fences typically reveals large numbers of geckos (Rodda 1991) that would seem to be ideal prey for small snakes. One possible explanation is that smaller snakes are less likely to be seen by human observers during fenceline searches, thus biasing captures towards larger snakes. However, this seems unlikely as the color and reflectance of BTS makes them very obvious when illuminated on a fence and a fence can be completely scanned with relative ease. An alternative explanation is that most fences are separated from forested habitat by open ground. If small snakes are somewhat loath to cross open ground, as suggested by the results above, then these small individuals may be largely filtered out of the pool of animals available for capture on fences. The relative absence of very large snakes from fenceline captures may be due to their relative scarcity in the population's sampled or low densities of suitable-sized prey (e.g., rats, birds) on fences at night. If large prey items are uncommon, then fences may hold few odors from these prey types and, thus, may be chemically unattractive to large snakes. Further observations and behavioral trials are needed to assess these hypotheses.

Engeman and Vice (2001) examined sizes of BTS captured on fences via spotlight searches in November and December of 1998. Although exact sample sizes are not given in their paper, the number of snakes taken from fences appears to be ~54, based on stated monthly means. They observed that only 3.7% of these captures were of snakes <750mm SVL, but that 81.5% of their sample was <1,000 mm SVL (for comparison with our paper, this is roughly equivalent to 1275 mm total body length). This trend is reinforced by the HIST dataset, which comprises roughly an order of magnitude more observations of snakes captured on fences (N = 568). Engeman and Vice (2001) used these results to conclude that “trapping was at least as effective for capturing small (sub-750 mm) snakes as was spotlighting fences.” We note that capture rate of small snakes using either method is relatively low as calculated by Engeman and Vice (2001), and that more recent intensive research reveals that trapping is ineffective for small juveniles (<700 mm SVL, Rodda et al. 2007). Capture rates of small snakes on fencelines are, therefore, higher than rates from trap captures – however, these rates are low compared to mid-sized snakes, and extremely low in relation to their probable abundances in the population being sampled (Rodda et al. 2007).

CONCLUSION

We conclude that long-term datasets of BTS captures via visual searches were largely concordant with intensive visual surveys of a geographically-closed population. These historical datasets, with large sample sizes from a variety of habitat types, may thus offer useful information when examining habitat-specific or temporal trends in various aspects of BTS behavior and habitat use. Our results indicated that small BTS were almost exclusively arboreal, while large snakes used arboreal and terrestrial habitats in roughly equal proportions. Juvenile BTS appeared to prefer to forage in tangantangan to a much greater extent than did adults, perhaps due to an abundance of small-bodied prey in this habitat type. Fenceline searches yielded very few small BTS, but fencelines may be used slightly more often by mid-sized snakes.

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